MODIFICATION OF SUB-ANTARCTIC FLORA ON MACQUARIE ISLAND BY SEA BIRDS AND SEA ELEPHANTS

By Mary E. Gillham

[Communicated by A. R. McEvey 14 July 1960]

Summary

An investigation of birds and seal colonies on Macquarie I. has shown a significant uniformity among the plants which colonize disturbed areas after the original vegetation has been depressed or destroyed.

Unlike most temperate Australian rookeries, it is probable that mechanical damage by trampling is of greater importance than the toxicity of heavy deposits of manure in the modification of the flora. This is largely due to the higher rainfall washing nutrients from the soil, the lower evaporation rates preventing excessive concentration of the soil solution and the fact that the Macquarie peat would retain water and act as a 'buffer' to chemical changes in a way that the Australian sands would not. It is no doubt contributed to, however, by the greater number and larger size of individuals in the Macquarie fauna.

This and the dominant life forms of mesophytic grasses and cushion plants (a latitudinal effect) brings the vegetation more into line with that of British bird islands than of temperate Australian ones, where the dominant life forms are succulent herbs with xeromorphic grasses in the S. and salt bushes further N.

Similarities between Macquarie and N. temperate rookeries are at specific level in some instances, plants common to both being the cosmopolitan *Montia fontana* and *Luzula campestris*, and the European *Stellaria media*, *Cerastium vulgatum* and *Poa annua* which are introduced on Macquarie I.

Poa foliosa, which is dominant on the Macquarie peats at low altitudes, is also dominant of the ground flora on peaty mutton bird islands off S. New Zealand where it has not been destroyed by grazing animals. In both areas it is characteristically associated with a species of *Stilbocarpa*.

Introduction

Since 1948 the Australian National Antarctic Research Expedition has maintained a research station at Macquarie I. (lat. 54½°S., long. 159°E.). The author accompanied the 1959-60 relief expedition to the island in December 1959 to investigate some of the interrelationships of the flora and fauna.

Macquarie I. provides a breeding and resting ground for the birds and seals inhabiting an area of sea as large as the continent of Australia. When ashore these animals are concentrated mainly in the *Poa foliosa* grassland around the coast—a strip about 50 m. long. They bring about quantitative and qualitative changes in the flora, but these are nullified to some extent by the humid sub-antarctic conditions.

The climate is more rigorous than in Australasian rookeries or those of similar latitudes influenced by the Gulf Stream in the N. Hemisphere. The specialized conditions brought about by large concentrations of animals, however, lead to comparable effects in widely differing climates and certain species are common throughout. These include plants both native and alien to Macquarie I.

Taylor (1955) has given a detailed account of the Macquarie vegetation and soils. The present work summarizes some of the modifications observed in rookeries visited during the 1959 relief expedition and relates these to the flora of rookeries in other latitudes. No account of rabbit effects is included, these having been dealt with in detail by Taylor.

A. Principal Effects of the Fauna

1 Manurial Factors

The vast populations of animals present on Macquarie I. deposit vast amounts of dung, particularly during the summer growing season, but this affects the vegetation less vitally than do smaller deposits in lower latitudes. This is largely due to climate.

The mean annual rainfall is high by Australian standards ($40\frac{1}{2}$ in.) and this, combined with the steep gradients and narrowness of the coastal plain, would facilitate leaching. The constancy of fall throughout the year [rain occurs on 330 days of the 365 (Law & Burstall 1956)] ensures that much of the dung is washed away as soon as deposited and before hardening into more weather-resistant form. Some of the most heavily affected areas, the larger colonies of royal penguins (*Eudyptes chrysolophus schlegeli*), are situated on permanently flowing streams, so that much of the guano gets washed directly to the sea.

Perhaps even more important than leaching are the high humidity and constantly low temperatures which cut down evaporation and prevent undue concentration of the soil solution. This concentration is of great importance to rookery vegetation further N., particularly in those parts of Australia suffering the dry summers of the Mediterranean climate. Drought effects there are intensified by the concentration of guano in the soil to toxic levels.

The average relative humidity on Macquarie I. is high [92% (Taylor 1955)] and only 10% of the readings fall below 70% (Law and Burstall 1956). The mean monthly temperature is only 40·2°F. and that for the warmest month (January) only 43·8°F. Winds are strong and persistent but are moist after travelling over many hundred miles of ocean, and mist and cloud are very prevalent.

In drier climates rookery plants have always to contend with residual guano from past breeding seasons, as well as current defaecation during the growing season which so often coincides with at least part of the period when the birds or seals are in residence. On Macquarie I. it is doubtful if manurial constituents remaining in the soil from one growing season to the next are sufficiently concentrated to inhibit normal plant growth.

At the end of the unusually dry month of December 1959 there was little evidence to suggest extensive killing of plants by fouling, although small areas of the coastal lithosere which lacked soil depth were seen to be suffering locally.

A third factor minimizing damage by guano is the steady accumulation of plant remains which disintegrate but slowly in the cool moist climate. An important property of the peat in this regard is its high power of water retention. Penetration of manurial constituents to the level of most absorptive is hindered in peats (Gillham 1956).

Where the effects of manuring can be divorced from those of detrimental factors such as trampling, there is evidence that they are beneficial rather than otherwise —as in cool moist climates of the N. Hemisphere. Members of coprophilous genera and families, principally *Poa* and *Caryophyllaceae*, are locally stimulated in such areas.

The endemic *Poa hamiltoni* is one of the most characteristically ornithocoprophilous species and is confined to the vicinity of penguin rookeries (Taylor 1955). It is particularly abundant among the otherwise dominant *Poa foliosa* at the margins of royal penguin colonies where nutrient-rich drainage waters seep out between the tussocks. It is also typical of colonies of rockhopper penguins (*Eudyptes chrysocome*) where its morphological habit and ecological niche are strongly reminiscent of those of the closely related *Poa anceps* var. *condensata* of New Zealand. The latter grows in central and northern New Zealand at the margins of gannet colonies and around the entrances of penguin, petrel and shearwater burrows.

No *poa hamiltoni* was recorded in colonies of gentoo penguins (*Pygoscelis papua*) which are of a more temporary nature, birds evidently moving to a new site before the plant can become established. The more ephemeral and more easily established *Poa annua* is an important constituent of the vegetation in these colonies and was absent from few of the guano-affected areas or seal wallows visited in the N. of the island.

The most characteristic caryophyllaceous coprophile is *Stellaria media,* associated in places with *Stellaria decipiens* and *Cerastium vulgatum* (= *C. triviale*). *Colobanthus muscoides,* common on coastal rocks, is resistant to both guano and trampling and is abundant in the nesting sites of Dominican gulls (*Larus dominicanus*), Antarctic terns (*Sterna vittata*) and coastal gentoo colonies. Few species live on these coastal rocks and they succumb to bird disturbance in the following order: *Stilbocarpa polaris, Poa foliosa, Puccinellia macquariensis, Colobanthus muscoides, Cotula plumosa.*

The last is not strictly a part of the rupestral climax flora but a pioneer phase which colonizes denuded areas when this flora is damaged. In bird-disturbed zones it often remains dominant as regeneration of less guano-resistant phases of the lithosere are prevented.

Pioneer *Cotula* on a stack denuded of *Poa foliosa* and *Colobanthus* 9 months previously in a salt storm was of very different form from that which colonizes the guano-fouled stacks. The former had small leaves, silvery with hairs, and formed a mat only a few cm. high. The latter has large leaves, less silvery because of the wider spacing of hairs due to cell enlargement, and forms dense mats up to 15 cm. high.

The foliage of *Cotula, Colobanthus* and the 3 *Poa* species is deeper green where affected by the nitrogen from guano.

Gentoo penguins nesting on the floating bog or 'feather bed' community of Handspike Point had little effect on the flora because of the high water table at the ground surface which diluted the guano as it was deposited. The rosettes of *Pleurophyllum hookeri* which stood up above the mat of bog plants were coated with guano but damage seemed to be superficial, affecting only the leaves which were replaced annually. The wet turf was dominated by bryophytes, lichens and dwarf monocotyledons and no qualitative differences could be discerned in the rookeries, no diminution of indigenous plants nor influx of coprophilous ones.

Gentoos on a drier part of this *Pleurophyllum* alliance had had a more potent effect, killing much of the locally dominant but rabbit-grazed *Agrostis magellanica.* The community was slightly more open than the wetter one and allowed entry of *Poa annua* and *Stellaria media.*

The flora of these 2 rookeries was more diverse and less specialized than that of any other rookery investigated and contained the following angiosperms:

Acaena adscendens	D	*Montia fontana*	W D
A. anserinifolia	D	*Pleurophyllum hookeri*	W D
Agrostis magellanica	W D	*Poa annua*	D
Callitriche antarctica	W	*P. foliosa*	D
Cardamine corymbosa	W D	*Ranunculus biternatus*	D
Colobanthus crassifolius	W D	*Scirpus aucklandicus*	W
C. muscoides	D	*Stellaria media*	D
Epilobium linnaeoides	W D	*Stilbocarpa polaris*	D
Juncus scheuchzerioides	W	*Uncinia riparia*	W D
Luzula campestris	W		

(W = wetter rookery, D = drier rookery)

The ornithocoprophilous green alga (*Prasiola crispa* ssp. *antarctica*, det. Womersley), members of which genus are widely distributed in seabird colonies in Australia, New Zealand and Great Britain, formed robust thalloid growths in every rookery investigated and was also found on guano-affected soil around isolated albatross nests inland.

2 Trampling of Vegetation

Mechanical damage to vegetation by trampling is probably the factor of greatest significance in the modification of the Macquarie I. rookery flora. This is largely due no doubt to the influence of climate in reducing the effects of guano, but is also related to the large number and size of individual animals inhabiting the rookeries. A bull sea elephant (*Mirounga leonina*) may be as much as 20 ft long with an estimated weight of about 4 tons (Csordas, personal communication).

The soft-foliaged plants of sub-antarctic latitudes are particularly vulnerable to trampling. Erect species suffer most, the brittle petioles and peduncles of *Stilbocarpa polaris* being most susceptible to breakage (Pl. III, fig. 2). The small-leaved, low-growing type of *Stilbocarpa* which can survive in the presence of rabbits is slightly more resistant to mechanical damage but is always in danger of extermination by increased rabbit attack.

Trampling is of greater significance as a destructive factor on Macquarie I. than it is in most Australian rookeries. The xeromorphic rookery plants of drier latitudes are often dwarf, with horizontal stems better fitted to withstand trampling than are erect ones, or are shrubby plants of the salt bush type which are sufficiently large for birds and seals to walk round or beneath them rather than over them.

Destruction of the indigenous Macquarie plants leads to an influx of mat plants, some perennial and some annual. These too are soft-leaved and may suffer damage, but their hemicryptophytic nature enables them to persist in many areas.

The mat and cushion plants of the plateau (which is dominated by *Azorella selago* and mosses) are of resistant life form but are exposed to less trampling than are the taller *Poa foliosa* stands of lower altitudes. Scattered nests of burrowing and surface-nesting birds occur on the plateau, but the chief tramplers are the sea elephants and penguins of the coast.

Destruction of herbage by penguins occurs up to 600 ft above sea level and rookeries may be large, up to 16½ acres and containing over half a million birds in one instance (Mawson 1943).

The most complete plant annihilation occurs in the large rookeries of royal penguins, but there is evidence to suggest that even these originated on soil bared by other means and spread subsequently as marginal plants were destroyed.

On the SE. coast birds are centred on the lower courses of steep creeks and the alluvial fans where the fall of these is checked at their junction with the narrow coastal plain. The colonies broaden at the lower levels where the divided drainage channels are a factor contributing to the opening up of the vegetation. The resultant penguin colonies have a series of V-shaped extensions leading uphill, 71% of which have broad creeks flowing into their upper extremities. Because of the steepness of slope these are dry for much of the time. (No detailed investigation was possible at this end of the island, but it is likely that the remaining 29% had smaller drainage channels not visible from the sea leading into them.)

Some of the rockhopper and gentoo colonies of this Hurd Point area are similarly situated, but these birds nest more sparsely than the royals, spreading through the tussock grass and creating less concentrated devastation.

All 3 species perch on *Poa foliosa* tussocks which eventually disintegrate to leave mounds of peat, but royals were seen to be doing this only at the margins of well-established rookeries or penguin highways and gentoos only in areas previously damaged by sea elephants.

It seems likely that the rock-hopping and tussock-hopping rockhopper penguins may be more suited to opening out tall undisturbed tussock vegetation than are the other 2 species. When not among rocks, rockhoppers prefer to nest beneath the tussocks and the traffic of birds between the *Poa* 'stools' forms drainage runnels and leads to a drop in soil level, so that the sheltering tussocks become elevated on columns of peaty soil.

Gentoos, on the other hand, prefer to nest on top of tussocks which have already been partially flattened by sea elephants. Both species may use considerable quantities of grass in the construction of their nests, but the rockhopper's nest is often no more than a collection of pebbles in a peaty hollow.

It is difficult to assess the amount of damage brought about by gentoos in tussock grassland because of the degenerate state of the community as a whole in the areas which they frequent. Apart from total or partial destruction of the tussocks on which the nests are built, however, it is likely that their effects are soon obliterated because of the temporary nature of the rookeries. Rockhoppers, like royals, return habitually to the same rookery which is usually too precipitate to be frequented by sea elephants, so their effects are cumulative and specific.

Sea elephants drag themselves indiscriminately both over and between tussocks but in most wallow areas a high proportion of the tussocks survive (Pl. I, II). (Living tussocks are used as back scratchers by moulting seals during December-March.) Areas which are in fairly constant use become denuded of all vegetation and no colonization by adventive mat plants is allowed to proceed very far.

Taylor (1955, p. 88) states—

> The seals do not arrive until the end of the summer, after the plants' growing period, and thus the vegetation is able to recover. Any damage done during the year is not in evidence at the beginning of the next summer, apart from permanent 'bog holes'.

This would appear to be an over-simplification, however, as many hundreds of seals, mostly young bulls moulting, were present on the tussock grassland during the author's visit (22-27 December 1959). According to Csordas, who has made a weekly census of seals in certain areas, animals are numerous among the tussocks throughout the spring and summer and a certain number are present during the remainder of the year. The more densely populated period (August–April) covers the plants' growing season and allows of little floristic regeneration except in areas temporarily abandoned by the seals.

All stages of degeneration and regeneration of the plant community were discernible in December 1959, and it is unlikely that the scars left by the animals could be obliterated by a single year's growth, even if a respite from seal damage was to occur during the growing season.

Plants other than *Poa foliosa* which survive in the wallow areas are almost exclusively hemicryptophytes or therophytes.

The endemic Macquarie I. cormorants (*Phalacrocorax albiventer purpurascens*) on North Head nest mainly beneath the lower limit of angiospermous vegetation but there is an outlier of the colony on a rock outcrop further inland. The original *Poa foliosa, Stilbocarpa polaris, Colobanthus muscoides* alliance which persists on unoccupied parts of the rock has been destroyed by trampling and defaecation in the cormorant colony. It has been replaced by *Cotula plumosa* and *Prasiola crispa* ssp. *antarctica,* together with the depauperate but still living remains of the *Poa* tussock.

The feeding grounds of Dominican gulls, which were identifiable by the accumulations of pink shells of *Cantharidus coruscans* (det. Macpherson), show the results of trampling. The dominant *Poa foliosa* becomes dwarfed and partially or wholly replaced by mat plants characteristic of earlier seral phases. In the more seaward areas *Cotula plumosa* becomes dominant with *Prasiola* and *Colobanthus*. Further from the sea *Agrostis magellanica* is likely to show the most marked increase, *Cotula* rather less.

Any effects of Antarctic skuas (*Catharacta skua lonnbergi*), which nest on small peaty mounds protruding from the 'feather bed' community or on cliffsides, are masked by the effects of rabbits. On the 'feather bed' itself trampling by gentoos and wandering albatrosses (*Diomedea exulans*) has negligible effects because of the resilient nature of the 'floating' turf.

Sooty shearwaters (*Puffinus griseus*) burrowing on North Head have worn tracks between the bases of the *Poa foliosa* tussocks and facilitated the entry of small ephemeral plants without materially altering the community structure. The steepness of slope minimizes the difficulty of becoming airborne so tracks are short, birds having only to reach a small clearing in the tussock before being able to take off.

3 Soil Disturbance

Destruction of vegetation exposes soil to erosion and the steep gradients on the coast increase the erosive power of drainage waters so that the slopes become scored with anastimosing channels. The fibrous structure of the peat and its almost perpetual moistness, however, minimize the amount of wind erosion as compared with that of sandier rookeries in less windy areas.

Differential rates of soil loss on coastal flats frequented by sea elephants leads to the formation of hollows from one to many metres across. These act as natural drainage basins and become filled with liquid mud and water (Pl. II, fig. 2). Such sites are favoured by moulting sea elephants but not all are in use simultaneously and undisturbed wallows become gradually recolonized. Their flora has been described by Taylor (1955).

At the end of a dry December there was insufficient liquid in many of the hollows for wallowing and seals were moving down to the edge of the sea more frequently (Csordas, personal communication). This entailed greater wear on the tracks but expedited the plant colonization of the drying wallows.

Tracks providing access to various parts of the Nuggets rookery of royal penguins may be cut down to a depth of 5 ft below the surface (Mawson 1914). The main penguin highways here follow the creek beds and the combined action of flowing water and continuous streams of penguins passing in both directions has removed all soil, although silt is able to accumulate in the shelter of marginal tussocks. The nesting sites which abut on to the tracks in places are also subject to a certain amount of flowing water and are worn down to the bedrock. Even during a dry spell the down of the chicks may become very fouled with peat stains from persistent puddles in the nursery areas.

Black-browed albatrosses (*Diomedea melanophris*) and light-mantled sooty albatrosses (*Phoebetria palpebrata*) construct their nests by scraping soil and vegetable matter towards them with their beaks as they sit. The nests investigated were on very steep slopes so that the resulting bare soil usually extended around only 3 sides, the outer side being sometimes occupied by a tussock which formed the basis of the nest.

Erosion from sooty shearwater burrows is prevented to some extent by the protective canopy of *Poa foliosa* but a few earth cliffs have been cut back into the hillside at the mouths of occupied burrows.

Taylor (1955, p. 91), in referring to burrows, states—'Undoubtedly they must cause some improvement in aeration and drainage'. It would be interesting to obtain further data on this point. Preliminary work in shearwater and petrel colonies off the coast of Wales has indicated that this is probably the case in the more permeable mineral soils but not necessarily in peats (Gillham 1956a).

The steep nature of the North Head rookery would ensure a rapid run-off of rainwater and absorption by only the surface layers of peat. Burrows leading in among the bases of the *Poa* tussocks would form natural points of entry for the water so that more absorptive peat surfaces could become saturated. Even in the less retentive peaty sands of the Bass Strait mutton bird (*Puffinus tenuirostris*) islands, burrows have been found to remain waterlogged long after the surface soil has dried out.

4 Plant Regeneration on Cessation of Biotic Disturbance

Although relatively few birds and seals are ashore during the winter season, temperatures are too low then for a big influx of winter annuals during the period of least disturbance. Such plant colonists as appear in the rookeries must compete with the animals during the brief summer growing season, so plant regeneration is patchy and determined by local movements of the fauna from one area to another.

Annuals are the obvious first colonists and the periods of respite are often not long enough for the regenerative succession to proceed beyond these to the perennials of the undisturbed climatic climax flora.

With light but fairly persistent animal disturbance, as at the margins of royal and rockhopper penguin colonies, the guano has a selective rather than a wholly repressive effect and annuals such as *Poa annua* become partially replaced by coprophilous perennials such as *Poa hamiltoni.* This is a plagiosere or deflected succession with the end point of *Poa hamiltoni* differing from the normal end point of *Poa foliosa.*

Return from *Poa annua* to *Poa foliosa* is most likely to occur when the deflective factor has been entirely removed as in vacated gentoo colonies and the large isthmus colony of king penguins (*Aptenodytes patagonica*). The latter colony was exterminated by sealers about 1850, but all traces of the rookery had disappeared by 1911, as had traces of a royal penguin rookery in Caroline Creek in less than 40 years (Taylor 1955).

The first stage of the hydrosere in the abandoned sea elephant wallows consists of a felt of green algae forming a crust on the surface of the drying mud. The earliest angiospermous colonist is a lax aquatic form of *Callitriche antarctica*. As the mud dries the *Callitriche* produces the more compact shoots of the terrestrial form and part of the mat becames replaced by *Poa annua*. *Cotula plumosa* follows in the moister areas or may be the primary colonist in drier areas. *Poa annua* and *Cotula* are the most characteristic species of the seal wallows apart from the dominant *Poa foliosa*. *Prasiola* is also abundant.

In later successional phases *Cotula* and *Montia fontana* may be co-dominant with little *Callitriche* or *Poa annua* remaining. Other less important species in this regeneration complex are *Stellaria media, S. decipiens, Cerastium vulgatum* and *Cardamine corymbosa*. If disturbance continues to be withheld, a low growth of *Stilbocarpa polaris* appears and the community finally returns to *Poa foliosa* (Pl. III, fig. 1).

Lush growths of *Callitriche, Montia, Cotula, Poa annua* and *Vaucheria* sp. colonize the margins of peaty channels which drain the nutrient-rich mud and water from the bog holes.

The drier phases of the wallow succession are characteristic of those occurring throughout the tussock areas when biotic pressure is alleviated. Annuals are predominant in the earlier successional phases, 3 of them aliens introduced originally by the sealers but now occupying the Macquarie counterpart of the ecological niche which they occupy in bird and seal colonies of the N. Hemisphere.

On coastal rocks *Colobanthus muscoides* may appear between the *Cotula* and *Poa foliosa* phases of the succession or may form 'caps' on the denuded summits of *Poa* tussocks worn bare by seals or gentoos.

Further from the coast but still in tussock areas *Acaena adscendens* increases in the vicinity of nests. Taylor (1955, p. 118) attributes this to the wetter situation by nests and adaptation of the fruits to bird carriage. *A. anserinifolia* is present on the island, occuping rabbit-grazed areas as in lower latitudes, but the ecological niche which it occupies in rookeries of lower latitudes is occupied on Macquarie I. by the apparently equally coprophilous but more water-resistant *A. adscendens*.

Nests of black-browed albatrosses had been occupied for only about 9 weeks when investigated and the chicks were still small, but already colonization of the denuded soil around the nest base by mats of *Prasiola* and seedlings of *Cotula* had commenced.

Nests abandoned the previous season showed a 25% cover of seedlings. *Stellaria decipiens* was dominant, *Poa annua* and *Cardamine corymbosa* abundant and *Festuca erecta* and *Agrostis magellanica* occasional. From the sides of the nests depauperate shoots of *Poa foliosa* and *Stilbocarpa polaris* were sprouting from underground organs which had survived the breeding season. Among them were seedlings of the 3 species mentioned above, *Acaena adscendens* and *Ranunculus biternatus*.

A flat-topped non-flowering *Poa foliosa* 'stool' used as a resting place by a light-mantled sooty albatross was much damaged and its sides colonized by *A. adscendens*. No material had been scraped up onto the *Poa* 'stool' but the surrounding ground was fouled and showed incipient colonization by *Cardamine, Colobanthus, Cotula* and *Metzgeria*.

Small patches of the 'feather bed' community scraped bare by wandering albatrosses are soon covered over by the surrounding plants and no trace remained of a marked nest occupied 2 years previously.

B. Relationship of Macquarie I. Rookery Flora with that of other Latitudes

1 Stewart I. Region, S. New Zealand

Small mutton bird (*Puffinus griseus*) islands off Stewart I. (lat. 47°S.) often show dominance of *Poa foliosa* tussock in burrowed areas with a species of *Stilbocarpa* sp. (*S. lyallii*) again the most characteristic associate. This vegetation may be destroyed by grazing goats and deer just as it is destroyed on parts of Macquarie I. by grazing rabbits.

The principal floristic difference between the 2 areas is the presence of trees and shrubs on the New Zealand islands and the larger number of ferns (including the 3 species found on Macquarie I.). 58% of the Macquarie I. flora occurs also on the New Zealand islands.

The peaty substrate of the Macquarie rookeries resembles that of the sooty shearwater rookeries in the Stewart I. region rather than that of any seen in Australian rookeries. New Zealand seal colonies visited differ mainly in that the New Zealand fur seals (*Arctocephalus forsteri*) penetrate less far inland and the associated species are mainly ephemerals on the beaches—*Poa annua, Stellaria media,* etc.

2 Tasmanian Islands

The main feature in common between the Macquarie rookeries and those of the Tasmanian islands (lat. 40°-44°S.) is the predominance of *Poa* tussock. The Tasmanian *Poa* (*P. poiformis*) is more xeromorphic but forms a similar type of terrain with soil eroding from around the bases of the plants to leave the tussocks elevated on peaty 'stools'.

Higher temperatures in Tasmania give rise to a slower rate of peat accumulation and increasing variety of plant species. Many of the Macquarie annuals, both native and introduced, occur on soil bared by the fauna, but there is an increasing tendency for these to reach their maximum growth in spring and autumn rather than in summer.

3 Islands of N. New Zealand

In these regions (lat. 35°-40°S.) there is an increase of succulent herbs (mostly Aizoaceae) in the rookeries but *Poa* tussocks remain as an important element. Both broad-leaved and needle-leaved Poas are represented, *P. anceps* and *P. australis* (= *P. caespitosa*) being the commonest natives, whilst *P. annua* and other Macquarie annuals occur more or less throughout.

Other Macquarie grass genera, chiefly *Agrostis* and *Festuca,* are represented mainly by introduced species from N. temperate zones in the New Zealand rookeries. As in S. New Zealand, the chief divergence from the Macquarie type rookery is the importance of the arboreal habit.

4 Islands of Temperate Australia

In southern Australian rookeries (lat. 30°-40° S.) there is a progressive northerly change from *Poa* tussock to more drought-resistant succulents, but the tussock habit persists in sandy areas where genera such as *Spinifex, Bromus* and *Lepidosperma* are important.

The ubiquitous annuals are still present but occur mainly in winter when atmospheric conditions become sufficiently moist and the soil guano suitably diluted. Fur seals (*Arctocephalus dorifera*) in latitude 30°S. are able to bear their pups beneath the dominant succulent-leaved shrubs (*Nitraria schoberi* and *Atriplex isatidea*) so that trampling has the effect of damaging only the lower branches whilst the canopy remains almost unaffected (Gillham 1960).

The principal life form of subordinate species is again that of mat plants with a high proportion of annuals. Macquarie genera represented include *Acaena, Cotula, Crassula* and *Epilobium.*

5 Islands around Great Britain

The similar latitude and climate brings the rookery flora of Macquarie I. closer to that of the islands around Great Britain (lat. 50°–59° N.) than to that of Australian islands. Temperature modification by the warm Gulf Stream in the N., however, curtails peat formation to some extent and provides more favourable summer growing conditions.

The principal floristic features of rookeries in both areas are the lack of trees and shrubs and the predominance of mesophytic grasses and cushion plants. All the Macquarie grass genera are represented on the smaller British islands, *Agrostis, Festuca* and *Poa* being the most important.

The coprophilous annuals which have been introduced to Macquarie I. (*Poa annua, Stellaria media* and *Cerastium vulgatum*) are abundant in British bird and seal rookeries, as are the 2 cosmopolitan species found on Macquarie I. (*Montia fontant* and *Luzula campestris*). Genera with nearly related species in the 2 areas include *Callitriche, Cardamine, Carex, Epilobium, Hydrocotyle, Juncus, Ranunculus* and all the grass and Pteridophyte genera of Macquarie I., although Pteridophytes are not particularly characteristic of rookeries in either area.

Important rookery plants with closely similar habit and leaf form are 2 creeping members of the Rosaceae, *Acaena* spp. in the S. and *Potentilla* spp. in the N.. *Prasiola* is the most typical genus of algae in rookeries in both N. and S. temperate zones.

Just as locally heavy biotic pressure on the Macquarie coast causes the climatic climax of grassland (*Poetum foliosae*) to give way to a cushion plant (*Colobanthus muscoides*) and a herbaceous creeper (*Cotula plumosa*), so does locally heavy biotic pressure on the British coasts cause the climatic climax of grassland (*Festucetum rubrae*) to give way to a cushion plant (*Armeria maritima*) and various creeping herbs (Gillham 1955, 1956b).

Acknowledgements

My thanks are due to the Antarctic Division, Department of External Affairs, for allowing me to accompany the 1959 A.N.A.R.E. relief expedition to Macquarie I., and also to the Science and Industry Endowment Fund and C.S.I.R.O. Wildlife Survey Section for the provision of research grants. Information and assistance in the field were given by Miss S. E. Ingham, Dr S. E. Csordas and Mr J. Munro of the Antarctic Division and Mr K. Campbell of the C.S.I.RO. Wildlife Survey Section.

References

GILLHAM, M. E., 1955. Ecol. of the Pembs. Islds. III. Effects of grazing on the vegetation. *J. Ecol.* 43, 1: 172-206.

———, 1956a. Ecol. of the Pembs. Islds. IV. Effects of burrowing and trampling on the vegetation. *J. Ecol.* 44, 1: 51-82.

———, 1956b. Ecol. of the Pembs. Islds. V. Effects of manuring by colonial seabirds and mammals. *J. Ecol.* 44, 2: 429-454.

———, 1960. Alteration of the habitat by seabirds and seals in Western Australia. *J. Ecol.* (in press).

LAW, P. G., and BURSTALL, T., 1956. Macquarie I., *A.N.A.R.E. Interim Report* 14.

MAWSON, D., 1943. Macquarie I., its geography and geology. *A.A.E. Report.* Ser. A. Vol. 5.

TAYLOR, B. W., 1955. The flora, vegetation and soils of Macquarie I. *A.N.A.R.E. Report.* Ser. B. Vol. II.

Explanation of Plates

PLATE I

Stages in the degeneration caused by sea elephants in *Poa foliosa* grassland.

Fig. 1—Young sea elephants among *Poa foliosa* tussocks. Community open and plants fairly small but healthy.

Fig. 2—Moulting sea elephants in degenerate *Poa foliosa* community showing damage to foliage and flattening of mounds.

PLATE II

Stages in the degeneration caused by sea elephants in *Poa foliosa* grassland.

Fig. 1—Dry portion of seal wallow showing replacement of *Poa foliosa* tussocks by smoPoth mounds of dark peaty soil. Tentative colonization by *Cotula plumosa* on right of seals.

Fig. 2—Seal wallow.

PLATE III

Fig. 1—An advanced stage in the regeneration cycle on an area previously occupied by sea elephants. Non-flowering *Stilbocarpa polaris* overrunning central mat of *Poa annua* with healthy young *Poa foliosa* (the climatic climax dominant) advancing from the margins.

Fig. 2—Damage caused by a passing sea elephant to the brittle foliage of *Stilbocarpa potaris.*